Ontogenic Changes in Microhabitat Distribution of Juvenile Bay Scallops, *Argopecten irradians irradians* (L.), in Eelgrass Beds, and Their Potential Significance to Early Recruitment

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Abstract. Ontogenetic changes in the vertical distribution of a cohort of juvenile bay scallops, *Argopecten irradians*, on eelgrass, *Zostera marina*, were followed throughout the summer and early fall in two Long Island embayments (New York, USA). Despite site-specific differences in eelgrass height and density, more than 95% of post-settlement scallops remained attached above the bottom until they reached a shell height of about 11 mm. Over a 5-week period, scallops gradually relocated until, at a mean size of 31 mm, all occurred on the bottom. The decline in percent attachment coincided with a 5-fold increase (from 16 to 84 μmoles min^{-1} g muscle dry wt^{-1}) in the activity of octopine dehydrogenase (proposed here as an index of the scallops' capacity for burst swimming activity), and in maximum rate of increase in the shell aspect ratio. While attached to eelgrass, scallops were nonuniformly distributed, with greatest concentration at mid-canopy. Following disturbance, they rapidly regained above-ground position, attaining asymptotic heights within 3–10 h. This and prior studies suggest that the climbing behavior of the bay scallop is an adaptive response to high predation pressure at small sizes. Enhanced scope for activity (predator avoidance) may enhance survival of scallops at intermediate sizes, when they become too heavy to maintain elevation but have not yet attained effective refuge in size.

Introduction

Bay scallops, *Argopecten irradians*, which commonly inhabit shallow, sheltered bays along the east coast of the United States, are closely associated with seagrasses, particularly during their early life history. Planktonic larvae of this species settle and attach by byssus threads, primarily but not exclusively to submerged vegetation such as eelgrass, *Zostera marina* L.; adults occupy a wider range of habitats, including bare, sandy substrata. Thus, dependence on vegetation and habitat restriction appear to decrease with age and size, as has been shown for a variety of marine and freshwater fish that extend their foraging grounds beyond areas with plant cover once they achieve size refuge from predators (Ebeling and Laur, 1985; Werner and Hall, 1988).

In common with other pectinids such as the sea scallop, *Placopecten magellanicus*, bay scallops can attach byssally throughout life, but seldom do so as adults (Belding, 1910; Stanley, 1970). Attachment of juveniles is reversible and dynamic, because *Z. marina* blades have a high turnover rate and elongate rapidly, at a rate of up to 2–5 cm day^{-1} in the summer (Kemp *et al.*, 1987). In pectinids, byssal attachment and swimming represent antagonistic behaviors (Caddy, 1972). Ontogenetic changes in attachment and swimming capacity of pectinids have been related to morphological, hydrodynamic features of their shells, such as aspect ratio (shell length to height ratio), umbonal angle, and degree of auricle asymmetry (Stanley, 1970; Dadswell, 1990). Burst swimming, which provides scallops with a mechanism to avoid predators, is associated with the production of octopine in rapidly contracting adductor muscle tissue. This end reaction of anaerobic glycolysis, which serves an important role in replenishing NAD$^+$ and thus maintaining glycolytic flux during functional anaerobiosis in highly mobile molluscs such as scallops and cephalo-

pods, is catalyzed by octopine dehydrogenase (ODH), an enzyme functionally analogous to lactate dehydrogenase (LDH) (Gade and Grieshaber, 1986). Ontogenetic changes in the activities of glycolytic enzymes such as LDH and pyruvate kinase and their relation to swimming performance have been described in several fish species (*e.g.*, Somero and Childress, 1980), but changes in ODH activity throughout the life cycle of pectinids have not been previously documented.

As reviewed by Brodie *et al.* (1991), prey have evolved two types of defense mechanisms to curtail predation. The first type, predator avoidance mechanisms, involves spatial (*e.g.*, Palmer, 1983; Main, 1987; Werner and Hall, 1988) or temporal (*e.g.*, Kitting, 1985) segregation from predators to minimize the probability of predator-prey encounter. The second type, antipredator mechanisms, increases the probability of survival upon encounter with a predator. Antipredator mechanisms include morphological adaptations such as large size (Crowl, 1990), increased ornamentation or thickening of the shell (Vermeij, 1987), distastefulness, or behavioral responses (*e.g.*, escape response or immobility; reviewed by Main, 1987).

Bay scallops are epifaunal, incapable of complete or prolonged valve closure, and less protected by morphological defenses than other molluscs with heavier, thicker shells; thus they require alternate mechanisms to reduce their vulnerability to predators. Using tethering techniques, Pohle *et al.* (1991) demonstrated that aboveground attachment to the eelgrass canopy gives juvenile bay scallops a significant refuge from benthic predators. Yet the laboratory experiments these investigators conducted using artificial grass suggested that this refuge may be ephemeral because the ability to attach above the bottom decreased markedly over a narrow range of scallop sizes (about 10 to 20 mm). The distributional pattern of the epiphytic, above-bottom habit for juvenile *A. irradians* and the transition to the adult epibenthic habit have not been adequately described in the natural environment and are the focus of the present study.

Information about the rate at which scallops can regain an elevated position and the timing and size at which they lose this ability is important for several reasons. First, it is necessary for determining the relative profitability of different elevations within the eelgrass canopy in terms of growth and survival. Second, it is a prerequisite for predicting the relative vulnerability of scallops to predators during early ontogeny. Third, it is an important consideration in rehabilitating stocks of this commercially exploited species because, in several states on the east coast of the United States, rehabilitation efforts mainly involve planting juveniles in suitable nursery habitat.

This work has three objectives: (1) to describe temporal/ontogenetic patterns in the vertical distribution of bay scallops in two bays in the Peconic-Gardiners estuary (Long Island, New York, USA) which differ in eelgrass structure; (2) to determine the rate of relocation and the height attained by individual scallops in the eelgrass canopy following disturbance, as well as the effect of scallop density on their climbing behavior in the laboratory; and (3) to relate distributional changes observed in the field to the swimming performance of scallops, as assessed indirectly from shell morphometrics (aspect ratio) and from the activity of octopine dehydrogenase in the adductor muscle.

Materials and Methods

Laboratory studies

Juvenile scallops obtained from a local hatchery on 2 May and 1 June 1990 were maintained in a flow-through upweller system at SUNY's Flax Pond Marine Laboratory until ready for use in experiments. These were carried out in rectangular plexiglass tanks (basal area = 31.5 × 78.5 cm) provided with recirculating, filtered (1 to 5 μm) seawater introduced immediately below the water surface (see Pohle *et al.*, 1991, for a detailed description of the experimental system). Eelgrass shoots were simulated with artificial mimics constructed of buoyant, green polypropylene ribbon (Synthetic Fibers Inc., Newton, PA) 0.5 cm in width, woven into plastic VEXAR mesh at a density of 500 shoots m^{-2}, and buried under about 5 cm of clean sand. Seawater was kept at 19° to 23°C and 26 to 28 ppt salinity with a cooling system and freshwater dilutions, respectively. White fluorescent lamps provided artificial 12 h:12 h (light:dark) photoperiod.

A first set of experiments tested the effect of scallop stocking density on the overall success of attachment to vertical substrates. Three experiments were conducted using scallops averaging 9.3 mm in shell height (H, greatest distance from the umbo to the ventral margin), each with density treatments of 300, 100 and 50 scallops per tank (1213, 404, and 202 scallops m^{-2}, respectively) on 11 May ($\bar{H} \pm SE = 8.6$ mm ± 0.09), 28 June ($\bar{H} \pm SE = 10.0$ mm ± 0.05), and 1 July ($\bar{H} \pm SE = 9.2$ mm ± 0.06). Shell height was measured for a subsample of individuals, and scallops were then randomly distributed on the bottom of each tank (water depth = 30 cm; height of eelgrass mimics = 25 cm). The number of scallops attached to blade mimics and tank walls was recorded every 30 min during the first 3 h, every hour during the following 3 h, and at the end of 24 h.

A second set of experiments investigated individual, size-specific climbing behavior. Individually marked scallops were followed over time for 46–49 h. Their vertical position was recorded hourly during the first 5–6 h and at less frequent intervals thereafter. Individuals were
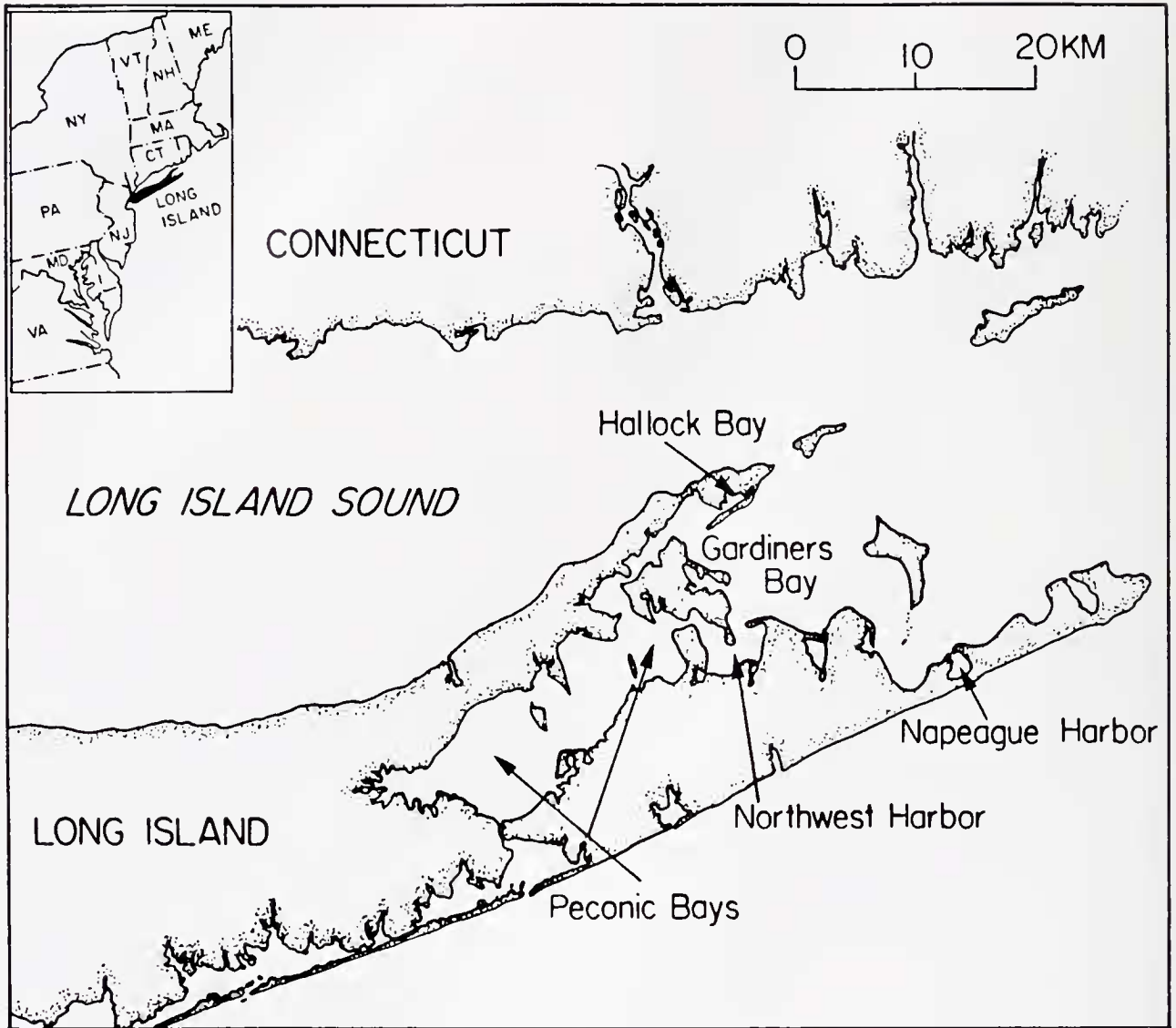
Figure 1.   Location of field study sites in eastern Long Island, New York.

identified with numbered, plastic-coated, miniature wire markers glued with Krazy Glue® to the upper valve at least 1 day before running experiments. For each trial, 20–22 scallops of a given size class were released into each of three experimental tanks (density = 89 scallops m^{-2}) containing eelgrass shoot mimics 50 cm in length. Three scallop size classes were tested on the following dates: 13.2 mm (SE = 0.07) scallops on 8 and 10 June, 5.7 mm (SE = 0.04) scallops on 11 and 13 June, and 7.2 mm (SE = 0.04) scallops on 14 and 16 June. The coefficient of variation in scallop sizes within any given experimental tank never exceeded 13%. A preliminary experiment showed that the height attained by 7-mm scallops did not differ significantly between one tank containing eelgrass

mimics, canopy height = 50 mm and density = 500 shoots m^{-2}, and two tanks containing natural, transplanted eelgrass, canopy height = 50 cm and density = 224 shoots m^{-2} (ANOVA at 48 h, F = 1.104, df = 2, 61, P = 0.338).

Field studies

Vertical distribution of natural set. The vertical distribution of naturally occurring juvenile bay scallops within the *Z. marina* canopy was characterized throughout the summer and early fall of 1990 in two bays in eastern Long Island, New York, which contrasted in eelgrass shoot density and canopy height: Napeague Harbor (NAPH, 41°01′ N, 72°03′ W) and Northwest Harbor (NWH,

41°01' N, 72°15' W) (Fig. 1). Both study sites are shallow (about 1 m deep in NAPH and 2–3 m in NWH), well-mixed, and characterized by gentle slopes, sandy substrate, and fairly extensive eelgrass (*Z. marina*) beds, which supported productive bay scallop populations prior to the occurrence of "brown tides" in the region (Hickey, 1977; Eckman, 1987; Bricelj *et al.*, 1987). They have also been the target of scallop reseeding efforts in recent years (C. Smith, pers. comm., Cornell Sea Grant Coop. Extension, NY; Tettelbach and Wenczel, 1991).

Eelgrass densities at the study sites were estimated in the second week of September by counting the number of shoots contained in 25-cm^2 quadrats randomly deployed within the survey area. Surface water temperatures were recorded with a hand-held thermometer ($\pm$ 0.5°C).

Although scallop settlement was first observed in NWH in mid-July, sampling for determination of growth rate, vertical position, and percent attachment of the scallop population on eelgrass did not begin until 26 July, when scallops averaged 4.5 mm in shell height and could thus be readily sampled by divers. Sampling continued until 10 October at NWH and extended between 16 August and 19 September at NAPH. In each harbor, an area well within the eelgrass meadow was sampled weekly. The size of the area was about 200 m^2 in NWH and about 50 m^2 in NAPH.

At each sampling, divers collected 100 to 150 juvenile scallops by swimming along set transects. Using rulers, the divers obtained *in situ* measurements ($\pm$ 0.5 cm) of the vertical position (height of attachment above bottom) of each individual on the eelgrass blade, and the total length of the blade. Scallops found on the bottom were assigned a position of 0 cm. The organisms were placed into numbered, perforated plastic boxes and brought to shore, where their individual shell height was measured with digital calipers ($\pm$ 0.01 mm).

Subsamples of 30 to 100 scallops (depending on size) were transported live in coolers to the laboratory, where they were immediately frozen and stored at -70°C until further analysis. These scallops were individually weighed (total wet body weight) using an analytical balance ($\pm$ 0.1 mg), and lyophylized. Soft tissues were then dissected and weighed using a Cahn electrobalance ($\pm$ 1 μg) or analytical balance, depending on scallop size. Shell height and length (greatest anteroposterior dimension) were determined prior to dissection in order to calculate the aspect ratio.

Octopine dehydrogenase activity. Lyophylized tissues were stored with dessicant at -70°C until used for enzyme assays. The adductor muscle of individual scallops (including both catch and phasic portions) was dissected out, weighed, and used for determination of octopine dehydrogenase (ODH, EC 1.5.1.11) activity, because more than

97% of the total activity in whole scallop homogenates is found in this tissue (Baldwin and Opie, 1978).

Powdered muscle samples (*ca.* 1 mg) were homogenized with a sonicator probe (Bronwill, Biosonik III) in 1 ml of 100 m*M* Tris-HCl buffer (pH 7.5) containing Triton x-100 (1% v/v). Homogenates were cooled in ice/water (0–2°C) during, and for a 30-min incubation period following, sonication. They were then centrifuged for 30 min at 1°C and 16,000 $\times$ *g*. The supernatant was decanted and assayed for ODH activity at 25°C by following changes in absorbance at 340 nm due to the oxidation of NADH, using a Milton Roy Spectronic 1201 spectrophotometer equipped with a thermal cell controlled by an external, recirculating water bath. Activity was determined by dividing the rate of change in absorbance by the extinction coefficient ($\epsilon_{340} = 6.23$ m*M*$^{-1}$ cm^{-1}) as described by Fersht (1985). All determinations were made in duplicate, using 50 μl of tissue extract in a total extraction volume of 1 ml, and were completed within several hours of tissue preparation. The composition of the reaction mixture and the concentration of the reactants were those reported to yield maximum enzyme activities (Baldwin and Opie, 1978): 1 m*M* sodium pyruvate, 0.1 m*M* NADH, 10 m*M* L-arginine and 100 m*M* tris-maleate buffer (pH 7.0). No controls were run for nonspecific activity because previous studies have demonstrated that in scallops, including *A. irradians,* the contribution of lactate dehydrogenase to the oxidation of NADH is negligible (Baldwin and Opie, 1978; Grieshaber, 1978; de Zwaan *et al.*, 1980; and Chih and Ellington, 1983).

Relocation experiments. Experiments designed to test the ability of juvenile scallops to relocate (climb and reattach) to eelgrass blades following dislodgement were carried out in Northwest Harbor and within sandy habitat in Hallock Bay (41°02' N 75°15' W; mean depth at low tide = 0.5 m; tidal range = 0.75 m) (Fig. 1).

The first relocation experiment was carried out in NWH on 9 August using scallops collected from natural populations at this site. Divers collected 150 scallops ($\bar{H}$ = 8.6, SE = 0.13) after determining their individual position on eelgrass as described earlier. Scallops were measured at the shore, individually numbered, and held in ambient bay seawater until released (within about 1 h of collection). Scallops were freely broadcast on the bottom of a previously marked plot within the eelgrass bed, where no predators were present. A diving survey around and inside the plot was carried out the following day (24 h after release) and the vertical position of each recovered individual was recorded.

A second relocation experiment was conducted using hatchery-reared scallops (10 mm), which were transported from the Flax Pond Laboratory to Hallock Bay (1.5 h) in coolers containing ice packs layered with wet newspaper.

Unmarked scallops were released by divers on 28 August within a 30-cm^2 area at the center of sandy plots (1 m × 2 m) within an eelgrass meadow averaging 32 cm in canopy height and 249 shoots m^{-2} in density. No natural scallop set was observed at this site in the year of the study. The perimeter of the plots was delimited by a galvanized chain (4.8 mm = 3/16 in. diam.), and plot location was marked with bright fluorescent subsurface buoys (Fig. 2 in Pohle *et al.*, 1991). Three hundred scallops were released in each of four experimental plots, and the percent attachment and vertical position of recaptured scallops were recorded after 3 h (plot 1), 5 h (plot 2) and 24 h (plots 3 and 4). Diver surveys covered a total area of 12 m^2 (a 2-m^2 plot plus a 10-m^2-perimeter area located 1 m around each plot). Plots were thus sampled destructively, rather than repeatedly over time, to avoid disturbance by divers.

Statistical analysis

Except where otherwise indicated, statistical analyses followed standard procedures described by Sokal and Rohlf (1981). Percent attachment data obtained from the three stocking density trials were pooled for each time interval and scallop density (50, 100, and 300 scallops per tank). Differences in arcsine-transformed percent attachment values obtained every hour between 1 and 6 h and at the end of 24 h were analyzed with a repeated one-way ANOVA (Wilkinson, 1990).

Differences in height attained on eelgrass mimics with scallop size were analyzed by a two-step procedure. The first step consisted of *a posteriori* multiple comparisons of the mean height attained by scallops (three trials pooled for each size) at 1, 3, 5, 10, 24, and 46–49 h. A Tukey-Kramer test was used on scallop sizes that had homogeneous variances (13.2-mm scallops), and the Games and Howell test was used for those with heterogeneous variances (5.7- and 7.2-mm scallops). In the second step, the position of smaller scallops (5.7 and 7.2 mm) was (l n + 1)-transformed to correct for heterogeneity of variances, and the mean height of the scallops on eelgrass was compared using a repeated two-way ANOVA (Wilkinson, 1990) with scallop size and aquaria as factors. Time treatments were selected on the basis of results of the multiple comparisons tests and fulfillment of criteria for homoscedasticity among samples (F_{max} test).

The degree of association between shell height and elevation of scallops attached to eelgrass blades in the field was measured with the Pearson product-moment correlation coefficient. All data gathered throughout the summer were included in this analysis, but excluding scallops found on the bottom, *i.e.*, at height = 0. The height attained, calculated as a fraction of total blade length to

normalize data for differences in canopy height between bays, was used to test for differences between the relative vertical distribution of scallops from NWH and NAPH, using the Mann-Whitney test for two independent samples.

Data from the relocation experiment conducted in Hallock Bay were analyzed by the *a posteriori* Games and Howell approximate test for equality of means, with height attained at each sampling time as the dependent variable. For the relocation experiment carried out in NWH, the nonparametric Wilcoxon signed-rank test for paired comparisons was used to test for differences in the mean position of scallops at the time of collection and 24 h following release.

Results

Laboratory studies

Scallop stocking density, over the range tested in this study, had no significant effect on percent attachment to eelgrass mimics ($P = 0.293$, repeated one-way ANOVA). Percent attachment averaged 80% 2 h after release and 85% by the end of 24 h, irrespective of stocking density.

Although scallops swam actively during the first 15 min following release into the experimental tanks, very few (< 1%) attached to the blades by swimming onto them. Swimming generally resulted in vertical rather than horizontal displacement. Scallops primarily gained an elevated position by crawling, as reported by Pohle *et al.* (1991). Downward crawling was never observed, suggesting that scallops may display negative geotaxis at this stage of their life cycle. Tracking of individual trajectories showed that, until they attained their final attachment position, scallops occasionally fell off the blades and had to re-initiate their ascent; but on average, over all trials, only 13% (range = 5 to 29%) fell to the bottom during ascent. Climbing behavior consistently showed two phases: rapid crawling during the first 4–5 h after broadcasting on the bottom, followed by a slowing or complete cessation of crawling. Mean crawling rates, calculated over the first 4 h for animals that did not fall during ascent, were 4.5 cm h^{-1} (SE = 0.8, $n = 156$) for small scallops (5.7- and 7.2-mm size classes) and 1.2 cm h^{-1} for 13-mm scallops (SE = 0.2, $n = 41$).

Laboratory experiments showed that the vertical distribution of scallops on eelgrass mimics was markedly affected by size. Within a 50-cm canopy, small scallops ($\bar{H}$ = 5.7 and 7.2 mm) reached a near-average asymptotic elevation of 20.4 and 18.8 cm respectively, 10 h after being released into the tanks (Fig. 2); larger scallops (13.2 mm) reached a near-asymptotic height of 6.0 cm after 11 h. Mean height attained by small scallops after 1 h was significantly different from that achieved after 24 h and
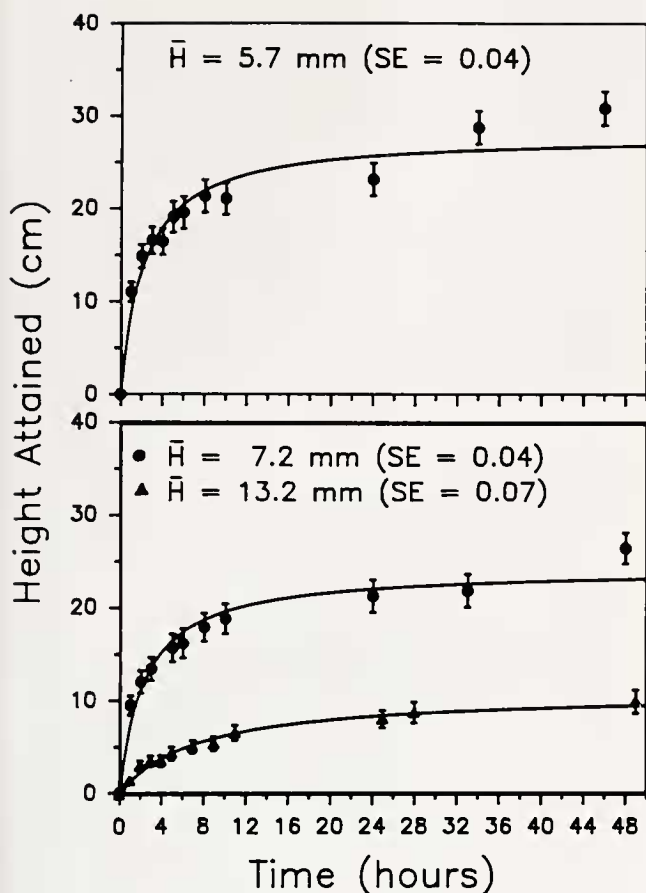
Figure 2. Temporal changes in the mean height above bottom attained by *Argopecten irradians* of three different size classes on eelgrass mimics in the laboratory (mean blade height = 50 cm). Data points are fitted to a rectangular hyperbolic function $(Y - aX/b + X)$. Vertical bars represent 95% confidence intervals.

Field studies

Vertical distribution of natural set. A single cohort of first-year *A. irradians* occurred in both embayments throughout this study (July–October), as indicated by unimodal size-frequency distributions obtained in NWH and NAPH over time. No significant new recruitment of post-settlement scallops was observed during late summer and early fall at either study site, except for a few new recruits (< 4% of the total) observed in NAPH in early September, although spawning in these embayments is known to extend throughout June and July (Bricelj *et al.*, 1987). Growth parameters (changes in total body weight

Table I

Results of repeated two-way analysis of variance for comparison of mean heights attained by Argopecten irradians *on eelgrass mimics*

A.

Source of variation	Degrees of freedom	MS	F	Significance
Between subjects				
Size	1	2.043	0.632	NS
Aquaria	2	3.185	0.985	NS
Size × aquaria	2	8.321	2.573	NS
Error	124			
Within subjects				
Time	5	21.173	62.309	***
Time × size	5	0.139	0.409	NS
Time × aquaria	10	0.327	0.963	NS
Time × size × aquaria	10	0.513	1.509	NS
Error	620	0.340		

B.

A posteriori multiple comparisons

5.7-mm scallops

Time (h)	1	3	5	10	24	46
Height attained (mm)	10.7	16.1	18.5	20.4	22.4	29.9

7.2-mm scallops

Time (h)	1	3	5	10	24	48
Height attained (mm)	9.5	13.4	15.7	18.8	21.2	26.4

13.2-mm scallops

Time (h)	1	3	5	9	25	49
Height attained (mm)	1.3	3.1	3.8	4.7	6.9	8.4

A. Scallop size (5.7 and 7.2 mm) and experimental aquaria (3 per size), with $n = 20$–23 scallops each) were used as testing factors. Runs were carried out on separate dates for each size under identical laboratory conditions. Comparisons were based on records for the same individuals at times = 1, 3, 5, 10, 24, and 46–48 h. B. Results of the Games and Howell approximate test for equality of means are shown for 5.7- and 7.2-mm scallops at selected sampling times. The Tukey-Kramer test was used for 13.2-mm scallops. *** = $P < 0.001$, NS = not significant at $P > 0.05$.

46–48 h (for 7.2- and 5.7-mm scallops, respectively), but not before ($P < 0.01$, Games and Howell approximate test for equality of means with unequal variances, Table IB). A Tukey-Kramer test of multiple comparisons also indicated significant differences ($P < 0.01$) in the mean position of larger (13 mm) scallops after 1, 3, or 24 h (Table IB). No significant size effects ($P = 0.428$) were found in the mean height attained by 5.7- and 7.2-mm scallops, or in that attained by scallops of the same size class located in different aquaria ($P = 0.376$, Table IA).

Mean elevation of small scallops (≤ 7.2 mm) coincided with mid-canopy height (0.57 of blade height; SD = 0.286, $n = 126$), whereas 22% of the scallop population was found near the top (upper 1/10) of the canopy, and none at the base of shoot mimics. In general, however, scallops were distributed throughout most of the length of eelgrass mimics at the end of 48 h (from 2.5 to 48 cm above bottom).

and dry tissue weight) of scallops collected in NWH are shown in Table II. Surface water temperatures at this site averaged 27°C in August and 23°C in September, attaining maxima during the second week of August. Temperatures at NAPH were within ± 1°C of those recorded at NWH. Shell growth rate throughout the study period averaged 13.3 and 12.5 mm month^{-1} at NWH and NAPH respectively. Based on these measured growth rates for juvenile scallops and a duration of 7 days for metamorphosis of dissoconch larvae into 1.5-mm plicated juveniles in NWH (Eckman, 1987), we estimate that initial settlement of this cohort occurred in the second week of July.

Densities of juvenile scallops were determined quantitatively only at NWH on 16 August and 20 September, when they averaged 16 and 14 scallops m^{-2} respectively. Although eelgrass shoot density and canopy height were 1.5 times higher in NAPH (mean density ± SE = 704 ± 35 shoots m^{-2}; mean canopy height ± SE = 38 ± 0.5 cm) than in NWH (density = 464 ± 29 shoots m^{-2}; canopy height = 23.5 ± 0.3 cm), temporal patterns in the percentage of scallops attached to eelgrass were very similar at both sites (Fig. 3), and therefore did not appear to be strongly influenced by differences in eelgrass structure. In NWH, 100% of the population remained attached to eelgrass blades until the second week of August, when scallops reached 11.2 mm in mean shell height. In NAPH, 100% attachment was also observed until scallops reached 11.3 mm, one week later than in NWH (Fig. 3). A 5-week transitional period followed, during which scallops relocated from their elevated position on eelgrass blades to the bottom. At both sites, more than 90% of new recruits were found on the bottom by the time they reached a mean size of 26–29 mm. Scallops found on the bottom

($h = 0$) are included in the calculation of mean heights plotted in Figure 4, showing clearly that in both bays the entire population had relocated to the bottom by the time scallops reached 31 mm.

At NWH, shell growth rate increased from 1.9–2.8 mm week^{-1} between 26 July and 30 August, when most of the scallops remained attached to the eelgrass canopy, to 3.1–4.6 mm week^{-1} during the period of relocation to the bottom (30 August to 23 September) (Table II), when attachment dropped sharply from 75% to 1%. Maximum shell growth during the first week of September coincided with a reduced rate of growth for soft tissues, which was equal to 30 mg week^{-1}, compared to values of 52 and 59 mg week^{-1} during the preceding and following weeks respectively (Table II). At NAPH, maximum rate of shell growth (4.5 mm week^{-1}) was recorded at the same time as in NWH. Allometric changes in shell shape with growth are evidenced by the sharp increase in the degree of shell elongation, as measured by the aspect ratio, between sizes of 10 and 25 mm, when scallops are gradually shifting from a byssate to a free-living habit (Fig. 5). Near-asymptotic values in this parameter (> 1.05) are attained at larger sizes.

Diver observations indicated that scallops exhibited a marked increase in swimming activity (diver avoidance response) during transition from an elevated position to the bottom, especially during the last week of August and the second week of September. This habitat shift was accompanied by qualitative changes in vegetation characteristics, notably an increase in the incidence of senescent (brown or discolored) *Z. marina* blades. Furthermore, in July, the drift red alga (*Gracilaria verrucosa*, was mostly restricted to the subtidal zone delimited by the lower eel-

Table II

Mean total body weight (TBW), mean dry soft tissue weight (DTW), and shell growth rates of juvenile bay scallops collected from natural populations in Northwest Harbor, New York, between 26 July and 10 October

Date	Temp. (°C)	TBW (mg)		DTW (mg)		Shell growth rate (mm wk^{-1})
		Mean	(SE; n)	Mean	(SE; n)	
26 July	25		–		–	
2 Aug.	27	83.3	(53.6; 49)	5.7	(0.4; 50)	2.2
9 Aug.	30	228.6	(15.0; 50)	15.7	(1.1; 48)	1.9
16 Aug.	29	389.4	(27.6; 51)	28.4	(2.2; 51)	2.6
23 Aug.	22	753.8	(53.0; 50)	57.7	(4.2; 48)	2.8
30 Aug.	27	1459.4	(82.8; 48)	109.3	(6.5; 48)	2.2
7 Sept.	25	1954.4	(128.6; 40)	143.8	(8.7; 48)	4.6
13 Sept.	25	2587.2	(177.6; 37)	193.2	(14.4; 37)	3.5
23 Sept.	20	4742.9	(276.2; 34)	342.4	(21.4; 33)	3.1
29 Sept.	22	5858.4	(423.6; 17)	424.8	(33.0; 17)	1.9
10 Oct.	21	8960.4	(538.6; 19)	608.8	(45.6; 16)	3.6

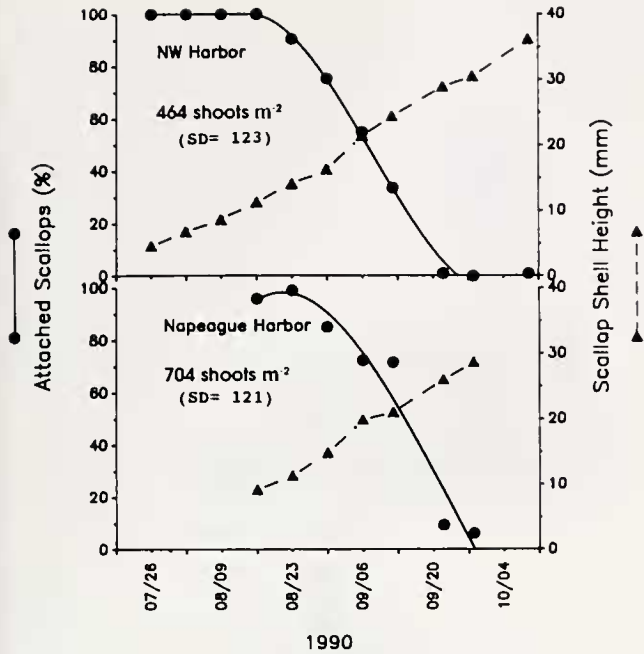Standard error and sample size are indicated in parentheses.

Figure 3. Temporal changes in mean shell height and percent attachment to eelgrass blades of a first-year cohort of *Argopecten irradians* in two eastern Long Island bays, during the summer and early fall of 1990. All standard errors are smaller than the symbol denoting mean shell height. Mean eelgrass (*Zostera marina*) shoot densities within the scallop distributional area are indicated for each harbor.

leptokurtic ($g_1 = 0.547$ and 0.151, and $g_2 = -0.101$ and -0.718 at NWH and NAPH respectively. Skewness was significant only at NWH ($t = 5.24$, $P < 0.001$), but kurtosis was significant at NAPH ($t = 2.95$, $P < 0.01$). The size-specific distribution of scallops, expressed as a fraction of total blade length, differed significantly between the two bays ($P < 0.001$, nonparametric Mann-Whitney test for two independent samples). In general, a larger proportion of the scallop population was located in the upper half of the canopy in NAPH than in NWH (about 50 and 30% respectively; Fig. 6).

Octopine dehydrogenase activity. Octopine dehydrogenase activity was used as an instantaneous index of the scallops' capacity for burst swimming activity. Within-individual variability in ODH activity, determined by assaying two to three replicate subsamples of ground adductor muscle from each scallop collected on 10 October (mean adductor dry weight = 266 mg), averaged 7%. Lowest mean enzymatic activity (16 μmoles min^{-1} g^{-1} adductor dry wt^{-1}) and lowest variation in activity among similar-sized individuals were measured in early August (Fig. 7), when the entire NWH scallop population ($\bar{H} = 6.7$ mm) remained attached to the eelgrass canopy (see Fig. 3). Mean ODH activity increased markedly between 30 August and 23 September, during relocation to the bottom, when attachment incidence dropped from
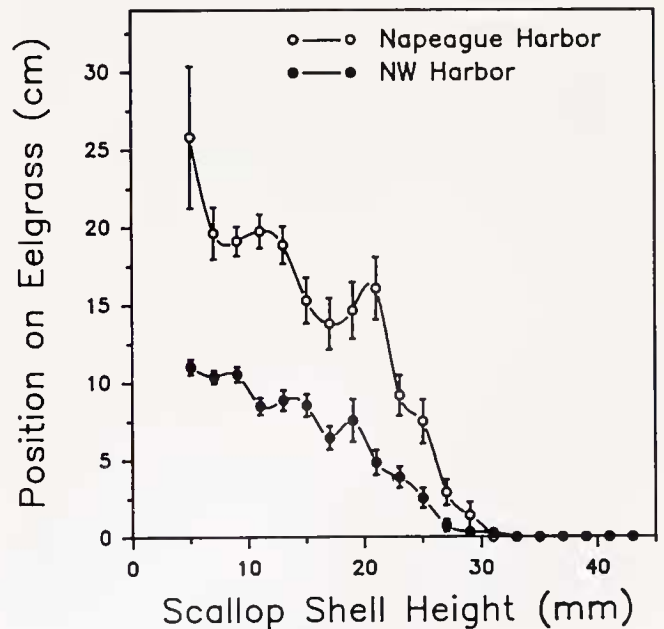
grass boundary, outside the scallop's main distributional area. However, by the first week of September, *G. verrucosa* was conspicuous throughout the entire scallop zone, intermingled with *Z. marina* or in irregular patches of 1 to 2 m^2.

Contrary to laboratory results, no significant correlation was found between scallop attachment height (excluding individuals found on the bottom) and scallop size in either NWH ($r^2 = 0.003$, $P = 0.176$) or NAPH ($r^2 = 0.001$, $P = 0.538$). This also differs from the laboratory results of Pohle *et al.* (1991), who found that the relative proportion of scallops attached to the upper vs. lower half of the canopy decreased monotonically between scallop sizes of 6 and 20 mm.

Although scallops were found distributed throughout the eelgrass canopy at both study sites, they clustered primarily at or around mid-blade height, between 0.3 and 0.5 of the canopy height, as indicated by the modes of the frequency distributions shown in Figure 6. This observation is in general agreement with laboratory results. The frequency distributions observed in the field departed significantly from normality (Kolmogorov-Smirnov intrinsic test for goodness of fit, $D_{max} = 0.048$ and 0.053 for NWH and NAPH respectively, $P = 0.01$). These distributions were skewed towards the upper canopy and were

Figure 4. Vertical position (mean height above bottom ± SE) of *Argopecten irradians* on eelgrass (*Zostera marina*) blades as a function of shell height, in two eastern Long Island bays. Scallops found on the bottom (height = 0) are included in calculation of the means; eelgrass canopy height = 38 and 23 cm in Napeague and Northwest Harbors respectively.
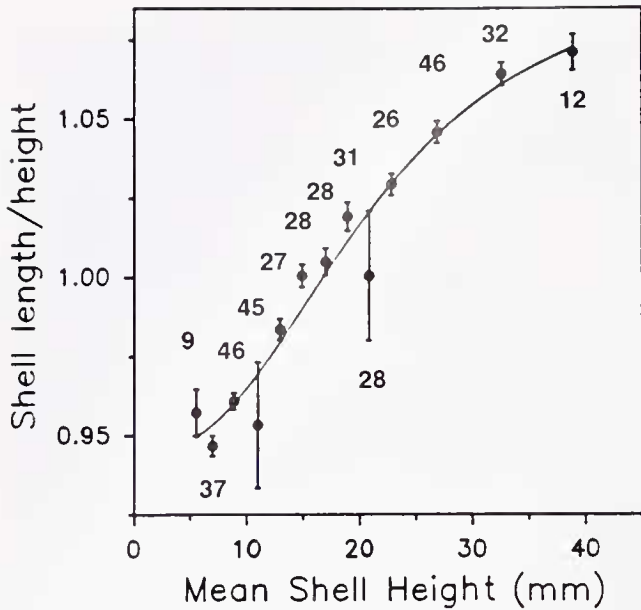
Figure 5. Aspect ratio (AR = mean shell length:height (H) ratio ± SE) with increasing shell height of a natural population of *Argopecten irradians* collected in Northwest Harbor. Sample size is indicated for each mean value. Fitted curve is described by the equation AR = (a − d)/[1 − (H/21.242)$^{-0.538}$ + d], where d = 0.944.

75% to 1%. Maximum mean values of 84 μmoles min^{-1} g^{-1} were recorded on 23 September, when scallops had reached a mean size of 29 mm, and appeared to decline thereafter.

Over the scallop size range sampled in this study, there was an overall, significant, positive relationship between octopine dehydrogenase activity (A) and muscle dry weight (W in milligrams), as described by the equation: A = 9.87 (SE = 3.52) W$^{0.35(SE=0.07)}$ (r^2 = 0.81; n = 57), determined using SYSTAT iterative nonlinear curve fitting (Wilkinson, 1990). It remains to be determined whether adult scallops exhibit a decline in ODH activities. High individual variability in ODH activity on any given sampling date may be partly attributable to the large variation in scallop sizes. A comparable three-fold range in the weight of the adductor muscles was obtained within any given sampling date throughout the study period.

Relocation experiments. Results of the relocation experiment carried out in NWH using individually marked natural set are shown in Figure 8. Forty-three percent of the scallops initially released (n_1 = 150, $\bar{H}$ = 8.6 mm) were recovered alive and 7% were found dead (crushed or with empty intact valves) by the end of 24 h. There was no significant difference between the mean position at time zero (collection) and 24 h following dislodgement (P = 0.063, Wilcoxon signed-rank test for paired comparisons; Fig. 8), although final height was lower than

initial height in 72% of scallops recovered on eelgrass, suggesting that 24 h may have been insufficient to achieve maximum, asymptotic height in this field experiment.

Relocation experiments carried out in Hallock Bay with hatchery-reared scallops ($\bar{H}$ = 10 mm) resulted in rates of attachment similar to those found in the laboratory with scallops of comparable size. Three hours after being released in the field, about 60% of the scallops recovered were attached to eelgrass blades, at a mean height of 8.7 cm (0.3 of canopy height), and these values remained relatively constant thereafter (Fig. 9). Maximum percent attachment and maximum height attained (when expressed as a fraction
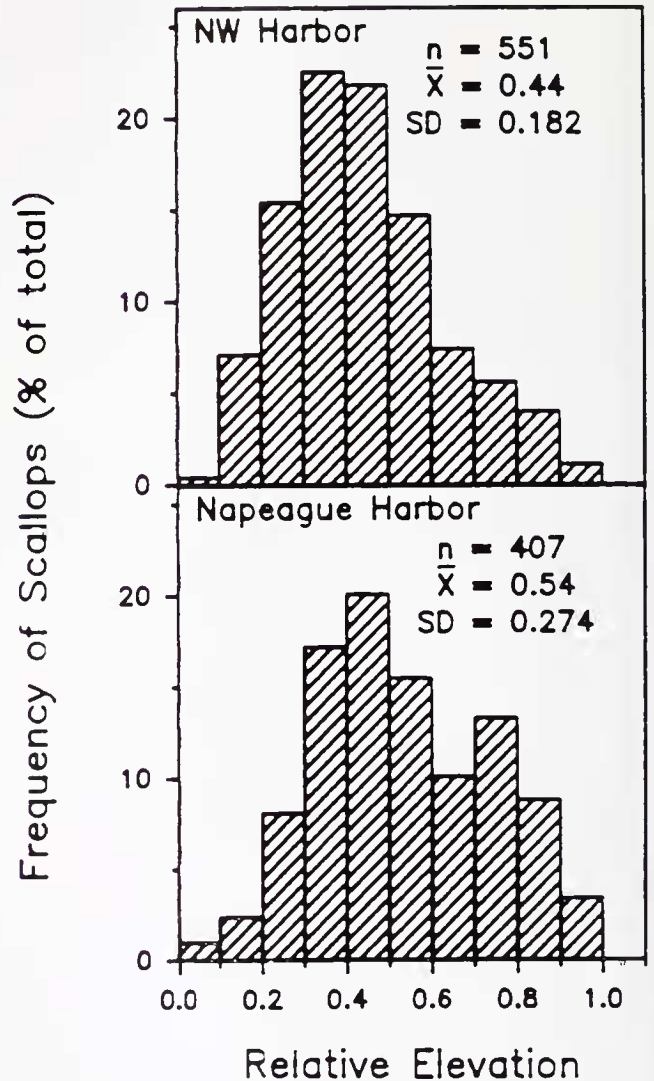

Figure 6. Distribution of juvenile *Argopecten irradians* attached in the eelgrass canopy. Relative elevation is expressed as a fraction of total blade length. All individuals collected above ground during the study are included, since there was no relationship between elevation and size of attached scallops.
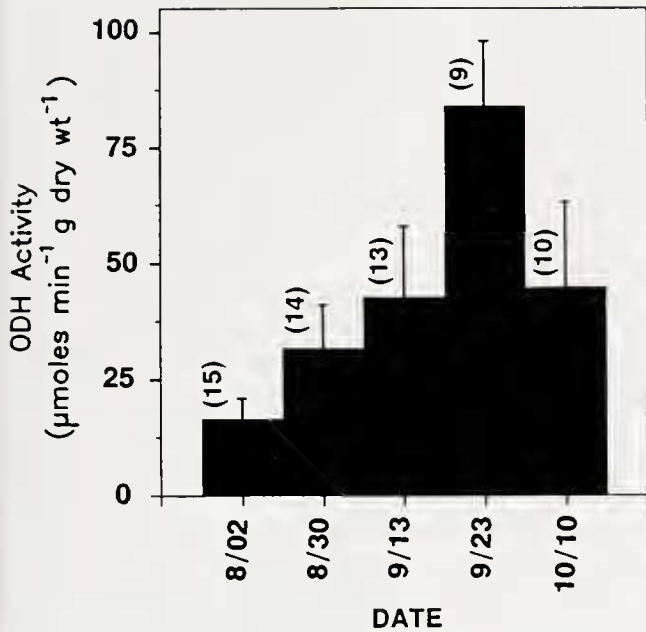
Figure 7. Octopine dehydrogenase activity (in μmoles of substrate min^{-1} g freeze-dried weight of adductor muscle^{-1}) of juvenile *Argopecten irradians* collected from a natural population in Northwest Harbor, between 2 August and 10 October. Error bars represent 95% confidence intervals around the mean for each sampling date. Total number of assayed individuals is indicated in parentheses; the 10 October mean includes three values obtained for pooled rather than individual samples.
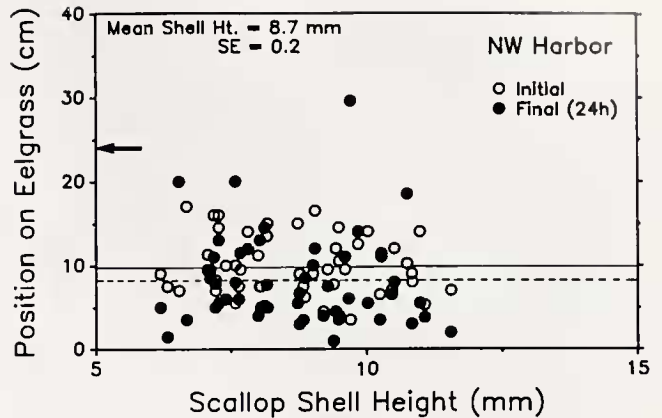

Figure 8. Above-bottom attachment height of individually marked, juvenile *Argopecten irradians* from a natural population in Northwest Harbor, before and after dislodgement from eelgrass blades. Open circles indicate scallop position at the time of initial sampling, and closed circles indicate position 24 h after dislodgement. Mean initial and final heights (9.9 and 8.0 cm) are indicated by solid and dashed horizontal lines respectively. The arrow marks the mean eelgrass canopy height at the study site.

of total canopy height), were thus lower than those of natural set in NWH and NAPH, and also somewhat lower than those obtained in laboratory trials (Fig. 2). No significant difference was detected between the mean height attained after 3, 5, and 24 h ($P = 0.178$).

Discussion

Laboratory and field results demonstrate that bay scallops can rapidly gain and maintain above-bottom position in the eelgrass canopy at sizes below *ca.* 10–15 mm. The adaptive significance of this behavior, which allows spatial segregation of juveniles from benthic predators and conspecific adults, may involve (a) enhanced survival through avoidance of predators and burial in unconsolidated sediments; (b) enhanced growth by positioning scallops in an optimum hydrodynamic regime that minimizes exposure to resuspended bottom sediments and maximizes food capture; or (c) a combination of these factors. Seagrasses are known to markedly reduce near-bottom current velocities and water flux (*e.g.,* Fonseca *et al.,* 1983; Eckman, 1987; Irlandi and Peterson, 1991) while generating increased turbulence at the water-canopy interface (Fonseca *et al.,* 1982; Gambi *et al.,* 1990), thus creating steep vertical gradients in the flow regime. Significant

variation in scallop growth rates with elevation within the seagrass bed was found by Ambrose and Irlandi (1992) and Borrero and Bricelj (in prep.), an effect that may be related to vertical gradients in food quality and quantity, as well as to flow.

The predator-refuge value of the eelgrass canopy for juvenile bay scallops has been well established (Pohle *et al.,* 1991; Ambrose and Irlandi, 1992). Refuge in elevation is effective in the presence of both nonswimming predators such as green crabs (*Carcinus maenas*), mud crabs (*Dispanopeus sayii*), and spider crabs (*Libinia* spp.) (Pohle *et*
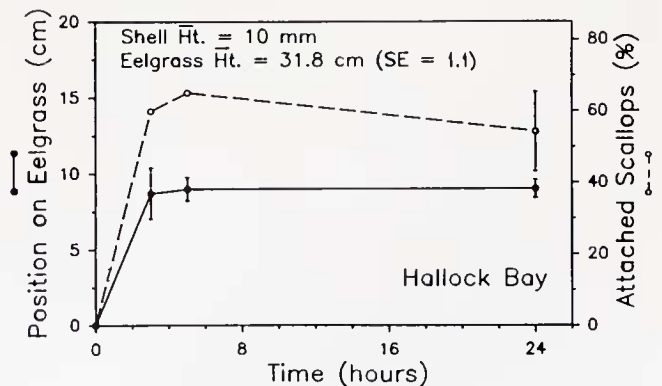

Figure 9. Time-dependent changes in percent attachment and attachment position on eelgrass blades (mean height $\pm$ SE) of hatchery-reared juvenile *Argopecten irradians* released in Hallock Bay, Long Island. (Total number of scallops recovered = 50 and 66 at 3 and 5 h respectively, and 95 and 60 from each of two plots at 24 h.)

al., 1991) and swimming, portunid crabs (Bauer and Bricelj, unpublished). The existence of a spatial, off-bottom refuge from predators in vegetated habitats was also described for the caridean shrimp *Tozeuma carolinense* (Main, 1987), and several gastropod molluscs. For example, juveniles of the freshwater snail *Planorvella trivolvis* and all life history stages of *Physella virgata* (both characteristically thin-shelled species) are known to crawl above the water line to avoid predation by crayfish, *Procambrus simulans* (Alexander and Covich, 1991). A similar predator-avoidance strategy was reported for the intertidal marsh periwinkle *Littorina irrorata* (Vaughn and Fisher, 1988).

During the period of attachment to eelgrass, most scallops were found concentrated at about mid-canopy height, with fewer individuals at the tips and bases of eelgrass shoots. In the field, this vertical distribution could reflect preferential aggregation of scallops at mid-height, or it could result from secondary effects such as differential predation pressure or physical disturbance with varying height. The reduction in scallop numbers near-bottom can be readily ascribed to the effects of benthic predation (Pohle *et al.*, 1991), but selective depletion in the upper canopy is harder to explain. Although this region is characterized by higher current velocities and turbulence intensity (Gambi *et al.*, 1990), free-stream velocities at the two study sites were relatively weak, typically attaining maxima ≤ 10 cm s^{-1} (Borrero and Bricelj, unpublished), and thus unlikely to cause selective dislodgement of scallops in the upper canopy. Eckman *et al.* (1989) found that juvenile bay scallops commonly experience current speeds ≥ 17 cm s^{-1} in seagrass beds in North Carolina, and remain attached to *Zostera* blades at flume velocities of at least 15 cm s^{-1}. We cannot, however, rule out the possibility that selective removal of scallops occurs during storm events. The northern puffer, *Sphoeroides maculatus*, a transient predator in some Long Island bays, can preferentially forage for scallops in the upper canopy (Tanikawa and Bricelj, unpublished). Greatest concentration of scallops around mid-canopy, however, was observed in both NWH and NAPH, even though *S. maculatus* was present during the summer of 1990 only in the former embayment.

Eckman *et al.* (1989) found that 5- to 15-mm scallops attained a mean elevation of 3.5 cm within an 8-cm mixed seagrass canopy in Core Sound, North Carolina. In our study, rates of relocation and patterns of microhabitat distribution (attainment of a near-asymptotic mean elevation at about mid-canopy height within 5 to 8 h) were similar for small scallops in the field and in the laboratory. This was the case despite the absence of food, predators, wind and wave action, and epiphytic cover in the laboratory, although fewer scallops (<3%) were found in the

top 1/10 of the canopy in the field than in the laboratory (22%). This similarity suggests that the scallops' distribution on eelgrass results from an adaptive behavior, rather than solely from mortality or disturbance operating after settlement. The findings of Pohle *et al.* (1991) further suggest that predator avoidance is the most likely selection factor for climbing behavior in juvenile scallops, although attachment height may also reflect preference within a vertically heterogeneous flow microenvironment.

The present study demonstrates that scallops between the sizes of about 14 and 29 mm undergo a gradual ontogenetic shift in habitat, from the emergent canopy to the bottom, over a 5-week period. The timing of this transition, which was remarkably similar in two nonadjacent bays, may be influenced by physical constraints that prevent larger scallops from maintaining elevation. Because bay scallops have no buoyancy mechanism and gravitational force scales in proportion to mass, larger scallops are expected to exhibit increasing difficulty in generating sufficient lift and/or strength of byssal adhesion to overcome the force of gravity and support their own weight. Irreversible relocation to the bottom, where predation risk is highest, is observed at a size of about 30 mm and a total body mass of about 5 g (weight in water was not determined in this study). At this size, however, scallops can attain complete refuge from the mud crab, *Dyspanopeus sayi*, a numerically dominant predator in these bays (Strieb, 1992), and partial refuge from other common crab predators (Tettelbach, 1986).

A sharp drop in percent attachment with scallop size is consistent with laboratory results obtained by Pohle *et al.* (1991) at a constant temperature, using eelgrass mimics. Percent attachment of scallops ≤ 10 mm was consistently high in both studies, ranging from 97 to 100% in NWH and NAPH, and from 83 to 98% in the study by Pohle *et al.* (1991). High percent attachment was also obtained in our laboratory stocking-density experiments (*e.g.*, 85% for 9-mm scallops), although maximum attachment was only 65% for 10-mm hatchery-reared animals broadcast in Hallock Bay. Variable attachment success may result from differences in condition and scope for activity between hatchery-reared animals and natural set, from selective predatory loss of unattached scallops in the field, or from a combination of both factors. This variability may have important consequences for the survival of cultured juveniles used in reseeding efforts aimed at stock enhancement. An inverse relationship between percent byssal attachment and scallop size (between 40 and 150 mm) was also described, both *in situ* and in the laboratory, in the sea scallop, *Placopecten magellanicus*, a species that attaches primarily to bottom features such as shell and gravel (Caddy, 1972).

Our qualitative observations suggest that swimming activity (escape response) of *Argopecten* increases at intermediate sizes, during the period of transition to the bottom. This corroborates observations made by Tettelbach (1991), who reported that adults and 2- to 7-mm spat of *A. irradians* swam infrequently compared to 15- to 35-mm juveniles. Dadswell (1990) identified three stages in the life history of the longer lived species *Placopecten magellanicus*, including a stage of highest motility at intermediate sizes (30 to 100 mm). Manuel (1992) also observed that juvenile sea scallops (< 10–12 mm) generally remain attached and are more reluctant to swim than larger juveniles. This author identified a discontinuity in the relationship between relative swimming speed and Reynolds number at scallop sizes of 12–16 mm; she attributed reduced swimming capacity below this size to increased drag and greater energy cost associated with swimming below this hydrodynamic threshold. Small juveniles were reported to swim primarily vertically, achieving little horizontal displacement (Manuel, 1992). This type of swimming behavior (vertical ascent), which was also characteristic of small (< 10 mm) *Argopecten* in our study, is expected to be relatively ineffective in avoiding predators, unless elevation allows scallops to be more readily advected away from predators by bottom currents.

In general, scallop species that are active and frequently swim have higher aspect ratios than those that rarely swim and remain byssate throughout life (Stanley, 1970). Furthermore, several scallop species that occur as free-living adults and byssate juveniles display an ontogenetic increase in both umbonal angle and aspect ratio (Stanley, 1970; Gould, 1971). This was confirmed for *Argopecten irradians irradians* in this study, where aspect ratios increased from about 0.95 to 1.07 at sizes between 5 and 43 mm. We are aware of no prior estimates of aspect ratios for juveniles of this subspecies. Our values are comparable to those reported for *Placopecten magellanicus*, a more proficient swimmer than *Argopecten*, over its life cycle (0.90 to 1.05 in the range 15 to 160 mm; Dadswell, 1990). An increase in aspect ratio with growth leads to a decrease in frictional drag and an increase in the lift coefficient of scallops. thus providing an advantage in swimming by partially counteracting the mechanical difficulties associated with increased weight (Gould, 1971).

The increase in swimming activity divers observed while the bay scallops were relocating to the bottom is presumably related to an increase in predator avoidance or dispersal potential and coincided in this study with a marked increase in adductor muscle ODH activity. *A. irradians* relies to a greater extent on anaerobic glycolysis via the octopine pathway to supply energy during burst activity (escape response) than do other scallops such as *Placopecten magellanicus* (de Zwaan et al., 1980) and *Chlamys opercularis* (Grieshaber, 1978). In these species, energy is primarily generated through breakdown of arginine phosphate, and octopine production is largely restricted to the recovery phase following exhaustion. Thus, in *A. i. concentricus*, glycolysis contributes up to 25–88% of ATP production during exhaustive swimming (Chih and Ellington, 1983). Therefore, in this species, ODH per gram of muscle can be interpreted as an index of weight-specific potential for anaerobic metabolism. Enzymatic activity of field-collected scallops showed a 5-fold increase between sizes of 6 and 29 mm, thus following a scaling pattern inverse to that of weight-specific aerobic metabolism, which typically decreases with increasing body size.

Future work should extend measurements of ODH activity to both smaller and larger scallop sizes and increase the sample size, given the large individual variability observed in this study. Ontogenetic changes in ODH activity and differences in scaling with body size between aerobic and anaerobic metabolism have not been previously studied in swimming molluscs. However, increased reliance on anaerobic metabolism for the maintenance of burst-swimming performance with increasing body mass, based on activities per gram of muscle of other glycolytic enzymes, has been described in finfish (Somero and Childress, 1980; Goolish, 1991).

In the present study, mean ODH activity in whole adductor muscle homogenates of *Argopecten irradians* attained a maximum of 84 μmoles min^{-1} g freeze-dried weight^{-1}, a value equivalent to about 17 μmoles min^{-1} g adductor wet wt^{-1}, assuming 80% water content of the adductor muscle. This estimate is lower than the value of 98 μmoles min^{-1} g wet wt^{-1} reported for *A. i. concentricus* of unspecified size (Chih and Ellington, 1983), and somewhat lower than values reported for other pectinids—i.e., 30 μmoles min^{-1} g wet wt^{-1} in *Pecten maximus* and *Chlamys varius* (Zammit and Newsholme, 1976), 58 μmoles min^{-1} g^{-1} in *Pecten alba* (Baldwin and Opie, 1978), and 26 μmoles min^{-1} g^{-1} in *Placopecten magellanicus* (de Zwann et al., 1980). All literature values cited were measured at 25°C for homogenates of the phasic (striated) adductor muscle, which typically comprises the bulk (about 80%) of total adductor weight (de Zwann et al., 1980), whereas whole muscle homogenates (catch+ phasic portions) were used in the present study.

In conclusion, the present study, in concert with prior related studies (Pohle et al., 1991; Strieb, 1992), supports the existence of three distinct phases during the bay scallop's early life history. During these phases, juveniles employ three different tactics to increase their survival: (1) development of upward crawling behavior by plicated and early juveniles ($\leq$ about 11 mm in shell height), enabling

them to rapidly relocate above a minimum threshold height on eelgrass blades to achieve spatial refuge from predators; (2) active escape response, coincident with substantial energy allocation towards shell growth and gradual loss of vertical refuge at intermediate sizes; and (3) attainment of a partial size refuge at sizes exceeding about 30 mm. Mortality rates of natural scallop populations before, during, and after relocation to the bottom are needed to determine the relative value of these successive refugia.

Acknowledgments

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